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Improving Lives: 50 Years of Crop Breeding, Genetics, and Cytology (C-1)

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ABSTRACT

During the past 50 yr, we have witnessed a revolution in the science of plant breeding, genetics, and cytology, and its impact on human lives (e.g., the Green Revolution). Because of increased productivity, breeding objectives evolved from predominantly improving yield to include greater quality and value-added traits. The discovery of the chemical nature of deoxyribonucleic acid (DNA), coupled with Mendelian genetics led to the refinement of quantitative genetics, the robust use of molecular markers, and transgenic crop plants. Cytogenetics elucidated the physical structure of chromosomes, aided trait and molecular mapping, and greatly enhanced the exploitation of genetic variation from wild relatives, as have transgenes and mutations. The fundamental process of selection has been improved by a better understanding of gene action, when to select, and better methods to select plants and analyze their relationship to the environments in which they grow. Single-seed descent plant breeding methods were popularized and evolved to doubled haploid breeding. Plant breeding, genetics, and cytology remain impact sciences that will continue to improve lives as part of the Evergreen Revolution.

"IF I HAVE SEEN FURTHER, it is by standing on the shoulders of giants."—Isaac Newton

SETTING THE STAGE: WHERE WE WERE IN 1955

In understanding the last 50 yr of Crop Breeding, Genetics, and Cytology (Division C-1), it is best to begin by understanding where we were in 1955. The world's population in 1955 was 2 781 183 648, with an estimated annual growth rate of 1.89% (U.S. Census Bureau, 2005). The population of the USA was 165 931 202, with an annual growth rate of 1.77% (U.S. Census Bureau, 2000). Fifty years later the estimated world population is 6 451 058 790 (232% more than in 1955), with an estimated annual growth rate of 1.15% and the population of the USA is 297 585 415 (179% more than in 1955; U.S. Census Bureau, 2005) with an annual growth rate of 0.92% (U.S. Central Intelligence Agency, 2005). In 1955, plant breeders, geneticists, and cytologists were within 10 yr of the World War II and many had served in it and all had lived through it. The population projections were clear and most people understood famine, deprivation, and poverty and remembered the Great Depression. They were also committed to change and to creating a new future.

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The state of our science was that the structure of DNA was elucidated in 1953 (Watson and Crick, 1953). Similarly rapid advancements were being made in cytogenetics and the genetic understanding or transfer of traits (Sears, 1953). Plant breeding had a long and successful history (Fehr, 1991; Stoskopf et al., 1993), but that is not to say that no new breeding methods were developed in the past 50 yr. The early work of Jones and Singleton (1934) and Goulden (1941) that led to single-seed descent breeding methodology was largely overlooked until it was redefined by Brim (1966). Similarly, the tools for the related doubled haploid breeding, which began in the late 1940s, were an omen of the robust methodologies that were created thereafter (Guha and Maheshwari, 1964; Chase, 1951; Kasha and Kao, 1970; Maluszynski et al., 2003).

BREEDING AND GENETICS: THEIR INTERRELATED ROLE IN AGRICULTURE AND 50 YEARS OF CHANGING ROLES

In the past 50 yr, agriculture has seen spectacular successes that include the Green Revolution (Everson and Gollin, 2003) in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) and the broad acceptance of single-cross hybrids in maize (*Zea mays* L.). While all of these advances include a significant genetic and breeding component, they also include significant improvements from other fields. For example, the high productivity of semidwarf wheat and rice cultivars was due to their having a greater harvest index and greater straw strength so that they could be grown with irrigation and much higher levels of fertilizer. Single-cross hybrid maize coincided with advances in herbicide technology and in the widening Corn Belt with conservation tillage systems and improved irrigation technology. To protect these higher yields, plant pathologists and entomologists helped plant breeders add disease and insect resistance to their cultivars. For those crops where end-use quality is important, cereal chemists and biochemists developed new methods and often changed technology to more effectively use new cultivars. Quality needs also required that breeding objectives change. Because plant breeders and applied geneticists obtain information from so many sources, almost all plant breeders and geneticists have worked in teams. While many early concepts of the breeding team had the breeder in the center of this cooperative crop improvement effort (e.g., Fig. 1.4 in Poehlman, 1979), many modern teams are more ecosystem based and have the cropping system specialist at the center of the hub and the plant breeder as one of the key scientists providing input. The focus has evolved from crop improvement to managed ecosystem improvement

Abbreviations: DNA, deoxyribonucleic acid; MAS, marker-assisted selection; NIR, near infrared reflectance; NIT, near infrared transmission; PCR, polymerase chain reaction; QTL, quantitative trait loci.

with its greater complexity, needs, and choices. Clearly, this trend of breeding and genetics becoming part of ecosystem management will continue as we approach the Evergreen Revolution.

Even within the breeding team, the role of the plant breeder has changed from one who did both breeding and evaluation to one who focuses on plant breeding, with agronomy or crop production specialists doing the final evaluations in different production schemes. Not only has the science become more complicated, but also the supporting technology (merely consider our increased ability to communicate) that enables scientists to work together has greatly improved in the last 50 yr.

Plant breeding and genetics also have evolved due to changes in our legal system as it relates to the right to patent life. The Plant Variety Protection Act (Public Law 91–577, enacted on 24 Dec. 1970; Fehr, 1991), which was required for signatories of the International Convention for the Protection of New Varieties of Plants (established in 1961 and revised in 1972, 1978, and 1991; International Union for the Protection of New Varieties of Plants, 2005), greatly expanded the intellectual property rights of plant breeders and the companies that employed them. As was intended, these legal changes spurred increasing interest in the private sector to expand their plant breeding efforts from predominantly crops sold as hybrids or populations to also include crops that were sold as purelines. This change led to increased privatization and commercialization, which has been most pronounced in Europe, where public breeding institutions were privatized or now survive on the basis of royalties. While the Plant Variety Protection Act and similar laws in other countries have spurred private sector research in cultivar development, the ultimate intellectual property right protection remains hybrid crops where they can be developed. Hybrid rice and cotton (*Gossypium hirsutum* L.) are routinely used in China and India, respectively, though hybrid wheat has been largely unsuccessful. Employment trends for plant breeders illustrate these changes. Although there are no figures for 1955, the estimated numbers of plant breeders in 1994 (Table 1 based data from Frey, 1996) and in 2001 (Table 2, Traxler et al., 2005) indicate that there are fewer plant breeders in both the public (state experiment stations and the USDA Agricultural Research Service) and possibly the private sector, with the greatest decline in public sector. The overall decline in plant breeders may reflect their enhanced productivity, the evolving nature of interdisciplinary research teams where plant breeding positions have evolved into related sciences, and the consolidation of plant breeding programs.

With the ability to patent life forms, especially transgenes, this trend toward increased privatization will continue. In many cases, the need to protect germplasm and breeding-related technology has led to a preference for partnerships between private companies over private–public partnerships. This, in turn, reduced the role of public universities as a supplier of germplasm and finished cultivars, the effect of which has been a concomitant reduction in the number of public breeders (Table 1 based on data from Frey, 1996; and Table 2, Traxler et al., 2005). The need for legal protection has also expanded the team that plant breeders and geneticists work with to include someone knowledgeable with patent, plant, and seed law. Virtually every breeder or geneticist working today has been exposed to material transfer agreements and codes of ethics to ensure the ethical use of plant materials.

Table 1. Estimated science person years by crop devoted to plant breeding research and development in the USA in the public (university and USDA-ARS) and private sectors. Plant breeding research and development includes basic plant breeding research, genetic enhancement, and cultivar development. Data were collected in 1994 and are from Frey (1996).

Crop category	University	USDA-ARS	Industry	Total
	Science person yr			
Cereal	155	34	703	892
Fiber	20	13	103	136
Forage	38	33	51	122
Fruit and vegetable	38	8	167	213
Grain legume (includes soybeans)	67	14	126	207
Lawn and turf	15	0	41	56
Leafy, bulbous, and stem vegetables	16	2	77	95
Medicinal, spice, and special crops	6	4	5	15
Oilseed	24	6	74	104
Ornamental	18	5	64	87
Root and tuber	45	12	24	81
Stimulant	13	2	5	20
Sugar	4	15	25	44
Temperate fruit and nut	50	23	32	105
Tropical fruit and nut	10	6	0	16
Miscellaneous	9	0	0	9
Total	528	177	1497	2202

In the previous sections we have described the trends have affected plant breeding, genetics, and cytology, with the understanding that many of the recent advances will be described in detail in papers describing the progress in Divisions C-7 and C-8. For the rest of this paper,

Table 2. Estimated science person years by crop devoted to plant breeding research and development in the USA in the public (university and USDA-ARS) and private sectors. Plant breeding research and development includes basic plant breeding research, genetic enhancement, and cultivar development. Data were collected from 2001 and are from Traxler and Acquaye et al., unpublished data, 2005.

Crop Category	University	USDA-ARS	Industry†	Total
	Science person yr			
Cereal	124	61	792	977
Fiber	20	11	122	153
Forage	27	27	39	92
Fruit and vegetable	19	7	78	104
Grain legume (includes soybeans)	56	22	185	263
Lawn and turf	16	0	9	24
Leafy, bulbous, and stem vegetables	6	7	36	49
Medicinal, spice, and special crops	3	1	1	4
Oilseed	20	6	35	61
Ornamental	39	25	54	118
Root and Tuber	30	11	9	50
Stimulant	11	1	6	18
Sugar	4	16	4	24
Temperate fruit and nut	33	18	12	63
Tropical fruit and nut	8	5	0	13
Miscellaneous	4	0	3	9
Total	420	218	1385	2022

† Data from industry may be incomplete, hence may represent the lower boundary of employment in that sector.

we will discuss how plant breeding and genetics have changed or stayed the same in practice during the past 50 yr. We have structured this paper the way a plant breeder would structure his or her breeding program, with emphasis on (i) defining breeding objectives, (ii) introducing genetic variation, and (iii) identifying superior new genotypes by selecting among the variants, with some comments relative to inbreeding for hybrid, population, or cultivar release. We have tried to include advances in genetics, cytology, and cytogenetics as appropriate. We conclude with a glimpse at our future.

DEFINING BREEDING OBJECTIVES

The basic outline of a plant improvement program includes three main components: defining breeding objectives, creating genetic variability, and identifying superior new genotypes. Other activities, including choice of parental material, methods for creating useful genetic variability, and strategies for evaluation and selection, relate directly to these objectives. A major consideration in developing breeding objectives is the ultimate use for which the crop is intended. During the past 9000 yr, we have domesticated crops to meet our needs for food, feed, fiber, and fuel (Harlan, 1992). It may seem that overall breeding goals for use of plants by humankind have changed little over time. What has changed is the diversity of species that supply each of our needs, particularly after the voyages of discovery and early plant exchanges, and how those specific traits are developed. One way to evaluate changes in plant breeding during the past 50 yr is to consider specific breeding objectives for various species during that time period.

Fifty years ago, the *Agronomy Journal* published invited papers that were presented at the 1954 meeting of the American Society of Agronomy in St. Paul, MN, in November 1954. An article on hybrid maize development in Europe and Mediterranean countries begins "Hybrid corn, a product of North American agriculture, has emigrated to all parts of the world. Directed against hunger and poverty, hybrid corn has started a peaceful, constructive revolution in Europe and Mediterranean countries" (Jugenheimer, 1955). The article indicates that use of hybrid maize nearly doubled from 1952 to 1953, replacing open-pollinated varieties in the region and accounting for 20 million bushels of increased production. The following two paragraphs also are quoted directly from the paper, because it is interesting to note where we were as a society in 1955 and where we are today. The author states the following (Jugenheimer, 1955):

> Many Americans are concerned over the apparent surplus of agricultural products accumulating in the United States. They feel that increasing the food supply in other areas of the world will compete unfavorably with American farmers. It is difficult for these Americans to realize that over half of the people in the world are hungry. Practically all of the better crop land of the world is now being farmed. Some acreage can be added by costly conservation, irrigation, and reclamation projects. However, increased food and feed production must come primarily from the land now being farmed.

This quote underscored the importance of increasing crop productivity. And so, it was not surprising that breeding objectives during the 1950s and 1960s related mostly to adaptation of crops to their production environments and to productivity and protection from diseases and pests. A cursory review of crop variety registration articles in *Agronomy Journal* for 1955 reveals objectives of improved grain yield for oat (*Avena sativa* L.), barley (*Hordeum vulgare* L.) and wheat; increased forage yield for bromegrass (*Bromus* spp.) and oat, lodging resistance for wheat, disease resistances in oat, bromegrass, and wheat, and increased seed oil content, ground cover, and uniformity of ripening in soybean [*Glycine max* (L.) Merr.]. Cultivar registration articles in *Crop Science* during 1965 included grain yield, insect and disease resistance, resistance to abiotic stresses [e.g., winter hardiness in barley and alfalfa (*Medicago sativa* L.)] and improved agronomic traits like straw quality in barley and rice, and reduced shattering and lodging in soybean. Quality traits like milling and baking quality in wheat, and improved fiber strength in cotton also were listed in the 1965 registration articles. Objectives in the 1975 *Crop Science* registration articles continued to relate mostly to adaptation in the area of production and resistance to disease.

Cultivar registration articles published in *Crop Science* during 1985 and 1995 uniformly included improved yield as the main reason for release of the cultivar, whether it was forage yield in orchardgrass (*Dactylis glomerata* L.), or grain yield in barley, wheat, soybean, or rice. Resistance to insects, disease, and abiotic stresses were also listed in combination with improved yield. Soybean cultivars for specialty food uses were listed in both years, indicating increased attention to seed quality characteristics for specific uses in that crop during the decade. The registration of 'Charleston' soybean in 1995 indicated its specific adaptation to highly productive environments due to the plant type and disease resistance traits of the cultivar (Cooper et al., 1995). One of the alfalfa registrations in 1995 also listed "high forage quality" as an improved trait in 'WL 525 HQ' Alfalfa (Cluff et al., 1995). Casler and Vogel (1999) indicated that breeding for increased nutritional value in forage crops produced significant increases in average daily gains of beef cattle (*Bos taurus*). They cite the importance of analytical instrumentation and methods that allow rapid and repeatable measurements for characteristics that are heritable and directly correlated with animal performance (Casler and Vogel, 1999). While there has been little or no increase in forage yield during the past 50 yr in many species, improvements in forage quality parameters like in vitro dry matter digestibility and neutral detergent fiber, coupled with improved protection from insects and diseases, have had important positive impacts on forage and livestock production (Casler et al., 2000; Casler and Vogel, 1999).

Plant breeding objectives relate to the needs of the producer to be able to grow the crop profitably, the processor for efficient development of products from the raw materials, and the consumer regarding acceptance and preference. For much of the past 50 yr, crops like

maize and soybean have been used primarily for feed. Emphasis has been placed on adaptation and productivity, with quantity generally more important than quality and environmental sustainability, though minimum quality standards are inherent, if not explicitly stated. Although disease and insect resistance have been goals for increased productivity especially in areas where pesticides are cost prohibitive, reducing the use of agricultural chemicals is increasingly promoted for its environmental benefits. As a general statement, it seems that breeding objectives in 2005 are focused more on quality traits; however, quality is defined by the end user, compared with the objectives of 50 yr ago. In addition, more desirable traits are being accumulated in individual cultivars. Such trait *stacking* is evident not only in multiple disease–pest resistance traits in grain and forage crops through multiple breeding cycles during the past five decades, but also in the transgenic input traits available in commercial cultivars for insect and herbicide resistance.

Examples of output traits in crop plants that have appeared in the past few years include maize and soybeans with low phytate phosphorus (Raboy et al., 2000; Wilcox et al., 2000), which have possible benefits for increasing feed efficiency and reducing unfavorable environmental impacts by reducing phosphorus in animal waste. Soybeans with decreased linolenic acid content in the oil provide stability and flavor benefits, as well as possible health benefits for consumers by eliminating the need for partial hydrogenation of the oil and production of trans fatty acids (Ross et al., 2000).

Breeding objectives also have changed from more traditional uses for feed and food crops to include industrial uses like production of polymers and biofuels. In switchgrass (*Panicum virgatum* L.), for example, breeding objectives include biomass production and composition traits that improve its use as a feedstock for ethanol production (McLaughlin et al., 1999; Cassida et al., 2005). Other efforts in currently grown crops and in new crops for bioenergy production are underway (USDA, 2005).

One technology that has had a major impact on plant breeding objectives during the past 50 yr is biotechnology (discussed in detail below). Have breeding objectives driven advances in biotechnology, or has biotechnology driven breeding objectives? Regardless of the answer, biotechnology has greatly expanded the source of genes, and the ability to track genes has greatly changed breeding objectives. The global area devoted to production of approved biotech crops has sustained a double-digit growth rate since their first introduction in 1995, growing more than 47-fold to an area of 81.0 million hectares in 2004 (James, 2004). In the USA today, transgenic cultivars and hybrids hold a large percentage of U.S. acreage in soybean, cotton, and maize. The initial commercial production of transgenic cultivars and hybrids in soybean, cotton, and maize represented 17, 15, and 8% of the total U.S. acreage in 1997, respectively. In 2005, commercial production of transgenic soybean, cotton, and maize represent 87, 79, and 52% of the total U.S. acreage, respectively (Economic Research Service-USDA, 2005).

The individual traits of herbicide tolerance and insect resistance have been the dominant traits in biotech crops during the past decade, with more recently stacked genes for herbicide tolerance and insect resistance deployed in cotton and maize showing increased growth (James, 2004). The author noted that 90% of the farmers who benefited from adoption of biotech crops were resource-poor farmers from developing countries. He stated "The continuing rapid adoption of biotech crops reflects the substantial improvements in productivity, the environment, economics, health, and social benefits realized by both large and small farmers, consumers, and society in both industrial and developing countries." A key example of a biotech-developed trait that is not herbicide tolerance nor insect resistance is Golden rice, which produces and accumulates β-carotene in the rice grain and is targeted particularly at developing countries of the world to improve nutrition and human health (Ye et al., 2000).

What is in the commercial trait pipeline (the current and future products of an institution) for commercial seed companies? Companies are using biotechnology to enhance traits important for the producer, processor, and consumer, including enhanced yield, pest control, disease resistance, resistance to abiotic stresses such as heat and drought, and improved compositional quality for processing and health benefits (www.monsanto.com/monsanto/layout/sci_tech, cited 14 Nov. 2005, verified 5 July 2006). Syngenta (Basel, Switzerland) plans to develop maize and cotton with improved insect resistance, wheat that is resistant to *Fusarium* spp., and production of human pharmaceuticals in plants (www.syngenta.com/en/about_syngenta/biotech_pipeline.aspx, cited 4 Nov. 2005, verified 29 June 2006). Numerous other products are in commercial pipelines. These products include soybeans with 80% oleic acid concentration to eliminate the need for hydrogenation of the oil and production of trans fats, and maize with enhanced digestibility and nutritional balance for feed efficiency with benefits of less waste and environmental impact. Maize and soybeans are being developed with enhanced composition for processing efficiency, polymer production, heat and drought tolerance, flavor, stability, and nutrition enhancements for food uses. Maize and soybeans are also being developed to improve the shelf life, flavor, and composition of meat, milk, and egg products from the animals that consume them (www.pioneer.com/usa/research/index.htm; verified 5 July 2006).

In 2005, breeding objectives for adaptedness and productivity remain most important for any crop, although these objectives are tempered by the need for total farm profitability, thus adding a farming and managed ecosystems approach. After all, it is the best-adapted and most productive germplasm that will likely provide the best means of deployment for existing and future traits derived from biotechnology. However, as the germplasm available to plant breeders increases, similarly the opportunities and breeding objectives will increase. Breeding objectives will continue to focus on those particular changes in elite material. As alternative crops are developed to fit new needs and market opportunities for

farmers and others, the primary emphasis will again be on adaptation and productivity of the new species in a farming system and will evolve to more quality orientation as the crop develops.

INTRODUCING GENETIC VARIATION

Regardless of the breeding objective, a critical step is identifying sufficient genetic variation to meet that objective. Simply, genetic variation must exist to achieve genetic improvement (Poehlman, 1979). Artificial hybridization and mutation-inducing procedures have been the traditional methods used to create genetic variation during the past 50 yr, and they remain the foundation for crop improvement. However, traditional methods have evolved with increased knowledge and technology, and new methods have also been developed to further expand our ability to identify and create genetic variation.

Creating Genetic Variation

Sources of genetic variation can be classified as (i) within species (intraspecies) (Harlan and de Wet, 1971); (ii) across species within a genus (interspecies) (Harlan and de Wet, 1971); and (iii) across different genera (intergenus) (Greene and Morris, 2001). Artificial hybridization has been and continues to be the most common method used to create intraspecies genetic variation.

With artificial hybridization followed by one or more generations of mating, the breeder creates genetic variation by allowing recombination to occur between chromosomes from different genotypes. Probably the most important success stories of using hybridization to create genetic variation in intraspecies sources during the past 50 yr were the introduction of semidwarf genes in wheat and rice and the genetic improvement of maize. 'Norin 10' (pedigree Fultz sel./Daruma//Turkey Red), the first of the short-statured, stiff-stalked, and high-tillering wheat varieties that helped to usher in the Green Revolution, was developed out of the genetic variation created by hybridizing a Japanese variety and two U.S. varieties, none of which had all the desirable characteristics of Norin 10 (Reitz and Salmon, 1968). In maize, the crossing of the Northern Flint and the Southern Dent races by 18th and 19th century American farmers led to the development of an entirely new race, the Corn Belt Dents (Wallace and Brown, 1956). The rich pool of genetic variability in this race was undoubtedly important in the approximate tripling of U.S. maize grain yields during the past 50 yr (National Agriculture Statistics Service, 2005).

A key issue in using hybridization to create new variation is selection of the parents. Despite the obvious importance of this issue, much more research has been done on methods of selection in breeding populations than on selection of parents to create these populations. A common trend in many crop species during the past 50 yr has been the increased importance of advanced cycle breeding, which Bernardo (2002) referred to as "inbred recycling." The replacement of landraces and plant introductions by elite lines as the parents was a recognition by breeders of the importance of creating breeding populations with good mean performance (e.g., the wisdom of the adage of crossing "good by good"). The concept behind recurrent selection of breeding populations was to improve the mean of the population and thereby greatly enhance the probability of obtaining segregates from this source that were superior to any of the original parents.

The other factor besides mean performance that breeders have considered in selecting parents is the genetic variability created by their hybridization. Schnell (1983; cited by Melchinger et al., 1988) combined genetic variance and mean performance in a single criterion called the usefulness criterion. Dudley (1984) recognized that in selection of parents, that not all loci are equal, but those in which the best allele is not present in the current breeding population should be given the greatest consideration. Numerous procedures have been developed for identifying the parents with these desirable alleles (Dudley, 1987; Bernardo, 1990; Metz, 1994). Despite the development of these new tools, selection of parents for hybridization probably remains for most breeders an educated hunch (Brim, 1966). Plant breeders often make as many crosses as resources allow, in hopes that one or more will yield commercial cultivars.

Artificial hybridization can also be used in combination with other methods to create genetic variation derived from interspecies sources. Other methods used during the last 50 yr to create genetic variation derived from the interspecies and intergenus sources include mutation breeding (Ahloowalia et al., 2004), embryo rescue (Comeau et al., 1992), cytogenetic chromosome manipulation (Fedak, 1999; Jauhar and Chibbar, 1999), and molecular chromosome manipulation via genetic transformation (Fraley et al., 1983).

As important as artificial hybrids are to create populations with novel genetic variation, hybrids are also important commercial products. The revolution with hybrid maize led to successful attempts to create hybrid rice (Yuan, 1992), hybrid sorghum (*Sorghum vulgare* L.) (Ross, 1965; Institute of Agricultural Sciences at Xinxian, Shanxi, 1972), hybrid cotton (Chaudry, 1997), and hybrids in many other lesser crops. As mentioned previously, attempts to create hybrid wheat have been less successful, as have attempts in barley and many other crops.

Advances in genetic improvement have also been made through mutation breeding using different methods of irradiation, a wide range of available chemical mutagens, and somaclonal variation generated through tissue culture and new strategies for screening mutations (e.g., TILLING; McCallum et al., 2000). Some of the key products resulting from mutation breeding over the last 50 yr have been demonstrated in a number of cultivated crop plants. Gamma radiation treatment of the rice cultivar 'Calrose' was used to select the semidwarf rice cultivar 'Calrose 76' (Rutger et al., 1977). Although Calrose 76 did not capture a huge portion of commercial rice production in California, it has been documented as the key parent used to develop subsequent high-yielding semidwarf cultivars in California (Rutger, 1992). More

recently, different mutation breeding methods have been used to produce imidazolinone tolerance in a number of different crops (Tan et al., 2005). Imidazolinone-tolerant crops developed through mutation breeding have been commercialized in maize via somaclonal variation generated through tissue culture, in oilseed rape (*Brassica napus* var. *napus*) via ethyl nitroso urea chemical mutagenesis, in rice via ethyl methanesulfonate chemical mutagenesis, and in wheat via sodium azide chemical mutagenesis. The mutations, not being transgenic, have been broadly accepted in all crops.

To create genetic variability derived from interspecies and intergenus sources, cytogenetic chromosome manipulation and molecular chromosome manipulation via genetic transformation have been employed with great success. Success with cytogenetic methods is best recognized for advances made in bread wheat and other *Triticum* species. Discovery of the chromosome pairing suppression gene *Ph1*, located on chromosome 5B, led to the recovery of progeny derived from wide crosses between *Triticum* spp. and alien species such as *Aegilops* spp., *Thinopyrum* spp., and *Agropyron* spp. These chromosomal manipulations have been accomplished using mutant lines with repressed *Ph1* activity and chromosome 5B deficient stocks (Jauhar and Chibbar, 1999). In addition, wheat–rye (*Secale cereale* L.) translocation lines produced spontaneously or by irradiation, which caused chromosomal mutations, have resulted in a unique source of genetic variability for use in wheat breeding programs. Rye chromatin present in these translocation lines has been a key source of disease resistance genes present in many current wheat cultivars in commercial production across the world (Rabinovich, 1998). The development of synthetic triticale cultivars presents a successful example of a much larger genome mutation derived from crosses between wheat and rye. Intensive triticale breeding programs were initiated in many regions of the world and led to the development of the first cultivar releases in 1968 (Oettler, 2005).

More recently, the success of various plant transformation methods has revolutionized our ability to create genetic variation. Plant transformation offers a limitless pool of genetic variation, because a gene from any organism can be cloned, modified, and engineered into the genome of any particular crop plant of interest. This science is developing rapidly. Now, not only are existing genes being mined from unrelated species, but also these genes are being modified by techniques such as DNA shuffling (Castle, 2004) to create potentially even superior transgenes. Since the first report of the production and recovery of genetically engineered plant cells in 1983 (Fraley et al., 1983), the commercial adoption of transgenic cultivars and hybrids in a number of cultivated plants has been staggering (see above). In summary, although artificial hybridization remains the plant breeders' most important tool for creating new breeding populations and genetic variation, during the past 50 yr there has been an expansion of the genetic resources available to plant breeders. Various types of chromosomal manipulations have made genes available from related species and genera that previously were not available via hybridization. Genetic transformation has made the complete biosphere a potential genetic resource.

Identifying and Measuring Genetic Variation

A key aspect of realizing genetic improvement through plant breeding continues to be our ability to identify and measure genetic variation. During the last 50 yr, genetic variation has and continues to be classified in terms of qualitative and quantitative traits. Achievements have been realized in our ability to identify and measure both qualitative and quantitative traits; however, it is clear that the genetic mechanisms of quantitative traits continue to be the most challenging to elucidate. In the 1950s and 1960s, quantitative genetics theory emerged as a powerful tool to measure and describe quantitative traits (Hanson and Robinson, 1963). Statistical methodology and designed matings were developed to allow researchers to calculate gene frequency, classify gene action, calculate heritability, and predict the genetic progress made from designed matings. The designed matings were very useful for genetic understanding, but tended to involve a limited number of lines, hence were unsuitable for the large numbers of crosses and populations often used in plant breeding.

At about the same time as statistical theory was being applied to quantitative genetics, discretely inherited morphological traits were used as genetic markers to develop chromosome linkage maps (Allard, 1956). From the initial application of morphological markers and linkage mapping, research aimed at identifying genetic variation in relation to quantitatively inherited traits expanded rapidly. In the 1980s, a new class of genetic markers termed molecular markers, which included isozymes and restriction fragment length polymorphisms (RFLPs; Botstein et al., 1980) were identified. The primary advantages of these new markers over the morphological markers was that they were more numerous and more polymorphic in most populations. Soon, efforts were underway to use these molecular markers to map the putative genes controlling quantitative traits, termed quantitative trait loci (QTL), by correlating trait variability with genetic marker variability measured in segregating populations (Stuber et al., 1987; Paterson et al., 1988). Newer types of DNA-based markers were developed in the 1990s through the use of polymerase chain reaction (PCR) technologies (Saiki et al., 1988). The large number of markers available today in many crops and their frequent high levels of polymorphism, coupled with improved statistical and biological methodologies made possible development of marker-dense linkage maps and more precise mapping of QTLs. Although QTL mapping efforts based on genetic recombination will continue to be used to identify genes segregating in discrete populations formed by artificial hybridization, new methodologies have also been developed to map QTL based on linkage disequilibrium (also known as association mapping).

In addition to mapping, molecular markers also have been used in a number of crop plants to measure the genetic diversity present in germplasm collections and/

or discrete populations. This measure of DNA based genetic diversity has been used in place of or in combination with the traditional coefficient of parentage measurement. The value of genetic diversity estimates based on molecular markers is that they are believed to have better theoretical assumptions than many of the previous methods of genetic diversity (e.g., Almanza-Pinzon et al., 2003; Fufa et al., 2005).

In considering genetic variation, the past 50 yr of cytological research has produced novel tools that have been used to synergize efforts to identify and clone important genes. Important cytological work has been conducted in many crops, but undoubtedly one of the best examples of cytological advances can be found in bread wheat and other *Triticum* species. As first reported in the 1950s, cytological methods and irradiation have been used to create valuable aneuploid stocks of wheat that include lines lacking single chromosomes, lines lacking specific chromosomal segments, lines with additional chromosomes, and chromosome substitution lines (Sears, 1953; Law, 1966; Endo and Gill, 1996; Morris, 1960–1984). These unique stocks have been used to physically map genetic markers to chromosomes as a comparison to recombination based genetic maps that aid strategies to clone specific genes (Erayman et al., 2004). In addition, unique genetic populations have been developed from these stocks that allow for QTL mapping of genes segregating on single chromosomes (Joppa et al., 1997; Shah et al., 1999; Campbell et al., 2003).

Success in efforts to combine cytogenetic and genomic technologies has resulted in the identification and cloning of several genes in a number of different crops including rice (Song et al., 1995), tomato (*Lycopersicum esculentum* Mill.; Martin et al., 1993), and wheat (Yan et al., 2003). In the last 10 yr, the expansion of genomic technologies has begun to revolutionize our ability to identify and measure genetic variation. Gene sequencing technology, first reported by Sanger and Coulson (1975), has improved considerably and allowed for the entire genomes of important crop plants such as rice to be sequenced (Goff et al., 2002; Yu et al., 2002). Bacterial artificial chromosome technology also has been developed to break plant genomes into smaller pieces that can result in targeted genome sequencing efforts and aid in the cloning of genes (Woo et al., 1994). Various gene expression technologies, such as microarray and quantitative PCR, have been developed that allow us to identify gene expression differences in relation to a particular trait and to study the expression patterns of specific genes.

Using Genetic Variation

The final and more applied aspect of genetic variation has long been maximizing the efficiency of using genetic variation to develop improved cultivars and hybrids. Efficiently capitalizing on the use of genetic variation continues to be an enormous challenge. Genetic variability is created and identified, but the dilemma faced by plant breeders is to separate the desirable variability from the undesirable. Many genetic mechanisms contribute to this difficulty; including linkage, pleiotropy, epistasis, and genotype-by-environment interaction. To better coordinate efforts to maximize genetic improvement during the last 50 yr, research programs using genetic variation essentially have evolved into two main categories: (i) cultivar and hybrid development, and (ii) germplasm enhancement. These two categories are generally classified by the source of genetic variability used to make genetic progress.

Cultivar and hybrid development programs have relied primarily on genetic variation created at the intraspecies level. In contrast, germplasm enhancement programs frequently have used genetic variation derived from interracial (e.g., maize), interspecies, and intergenus sources. These sources often have nonadaptive, wild, or weedy characteristics. History suggests that using genetic variation derived from interracial, interspecies, and intergenus sources require long-term efforts to select for desirable characteristics, while also removing undesirable characteristics. During the last 50 yr, germplasm enhancement programs have evolved into cultivar and hybrid development feeder programs by adding new germplasm into these elite programs. For major crops in 2005, genetic enhancement programs are predominantly performed by the public sector or cooperatively with the private sector, while intensive cultivar and hybrid development programs are primarily performed in the private sector for most of the major economic crop commodities. For less widely grown crops with little profit potential, the public sector continues to do both cultivar development and germplasm enhancement.

Germplasm development programs have relied on advances in several research areas to expand the creation of interspecies and intergenus genetic variation. These key research areas include tissue culture advancements to rescue embryos derived from wide crosses (Comeau et al., 1992), advanced cytological methods to confirm chromosomal transfer from distant sources (Fedak, 1999), and molecular biology methods that aid in introgression of specific genes or chromosomal segments via gene introgression and advanced backcross QTL methodologies (Tanksley and Nelson, 1996). Use of these technologies and others not mentioned within this text have allowed for germplasm enhancement programs to continue adding genetic variability into the intraspecies source of variation. One of the major challenges of the near future in germplasm development programs will be how best to utilize the massive amount of genomic information being accumulated on a number of plant species.

IDENTIFYING SUPERIOR NEW GENOTYPES

Once a breeder has clearly defined objectives and has identified or developed appropriate sources of genetic variation, then the actual selection work begins. There are two basic steps to this process. First, the selection units must be described or developed, which includes the generation (level of inbreeding) of selection. Sec-

ond, the criteria and methods for choosing the best among these units must be determined.

Selection Units

This term refers to the groups of plants that are evaluated and on which selection decisions are made. Thus, a selection unit could be an individual plant, a type of family, or even a land race. The type of selection unit often is dictated by the biology of the species. In a species with a long life cycle or in which making controlled pollinations is difficult, the choice of selection units may be quite limited. For example, nearly all the cultivars of foxtail millet [*Setaria italica* (L.) P. Beauv.] that are grown in the USA are selections from land races, because making crosses in this species is very difficult (Baltensperger, 1996). In some self-pollinated species, difficulties in producing sufficient seed for testing in early generations has led to selection, based on individual plants, for highly heritable traits or using advanced-generation lines as the primary selection units. In contrast, in an annual species that is relatively easy to self- or cross-pollinate, the choice of the types of selection units can be greater. For example, maize breeders have used individual plants, selfed progenies at various levels of inbreeding, crosses of these selfed progenies to different types of testers, and half- and full-sib families as the selection units. In breeding programs of many crop species, breeders employ multiple selection units. With pedigree breeding, for example, successive selection occurs among progressively more inbred families, basically changing from among and within family selection in the early generations to largely among family selection in the later generations.

With respect to the choice of selection units, what has changed during the past 50 yr? Beginning in the 1950s and continuing for several decades, considerable effort was devoted to determining the predominant types of gene action for yield and other important traits. A key question for maize breeders was the comparative performance of dominance and overdominance. The history of the research into this question was reviewed by Crow (2000). Some early research indicated that overdominant gene action was important for grain yield in maize (Comstock and Robinson, 1952; Gardner et al., 1953). However, subsequent research indicated that these early results likely were biased by repulsion-phase linkage and that the average level of dominance of genes controlling yield in maize was not in the overdominant range (Gardner, 1963; Moll et al., 1964). This finding and other research that showed the largest component of genetic variance in various types of maize breeding populations was additive variance (Hallauer and Miranda, 1988) led to an increased interest among some maize breeders to use families formed by self-pollination (e.g., S_1 and S_2 lines) as the selection units (Eberhart, 1970). Comstock (1964) concluded that selection among inbred progenies is expected to be nearly twice as effective as testcross selection for loci where overdominance is not present.

Several empirical studies have compared gains achieved with selfed progenies vs. testcross (hybrid) progenies (Horner, 1985; Tanner and Smith, 1987; Tragesser et al., 1989; Weyhrich et al., 1998), and Empig et al. (1972) published formulas for predicting gains both for selection schemes using selfed progenies as selection units and schemes using hybrid progenies. Interpretation of results from these types of studies can be problematic due to the confounding effects of genetic drift, particularly if the number of selection units that are recombined to form the next generation of the breeding population is small (Tragesser et al., 1989). Even though use of selfed progenies as selection units has been shown to be effective in improving general combining ability for yield in hybrid crops in some studies (Tanner and Smith, 1987; Ross and Hookstra, 1983), genetic correlations between inbreds and their hybrids typically have been low (Gama and Hallauer, 1977; Jensen et al., 1983). Using computer simulation and a model with 200 loci, two alleles per locus, gene frequency of 0.5, and complete dominance, Smith (1986) determined that the expected correlation between inbreds and their testcrosses were 0.34 or less. For hybrid crops, selection among testcross progenies has been the primary approach used by commercial breeders throughout the past 50 yr.

When selecting among testcross progenies, a key issue that has been debated during recent decades concerns the attributes of the ideal tester. Rawlings and Thompson (1962) advocated the use of a tester with low performance for the trait of interest because this should maximize the genetic variance among the testcross selection units. This idea was supported by Hallauer and Lopez-Perez (1979), who found that the variance for grain yield among S_1 testcrosses from an unimproved maize population was greater when the population itself was used as the tester compared with an improved version of this population and likewise was greater when a poor performing inbred selected from the population was used as a tester compared with an elite inbred from the population. However, Bernardo (2002) stated that use of a poor tester is not "practical" because the mean of the testcrosses is low. Hallauer and Lopez-Perez (1979) also determined that the variance among S_1 testcrosses was as high when the tester was an elite inbred from a different genetic background. In most commercial maize breeding programs, use of an elite, unrelated tester has been the standard practice for many years.

Generation of Selection

In discussing selection units, a related issue is the stage of inbreeding at which selection, either among selfed or testcross progenies, should be initiated. Although results from empirical studies specifically designed to investigate this question have been inconclusive, generally the idea of early generation testing has been supported in crops where dominance genetic variation can be used (Hallauer and Miranda, 1988). Perhaps the strongest support for early generation testing was been the large number of favorable outcomes reported for short-cycle recurrent selection schemes in numerous crops (Hallauer, 1981). A theoretical basis for support of early generation testing was provided by Bernardo (1992),

although both he and Johnson (1989) cautioned breeders against using a high selection pressure in early generations, particularly for a trait such as yield with low heritability. Interest in early generation testing was sparked by the high cost of testing and the desire to focus resources early on in the breeding program on the most promising genetic material. That is, the issue of early generation testing was an economic issue.

In self-pollinated crops, the value of early generation testing is more ambiguous (Cregan and Busch, 1977), selfing is natural, and very efficient breeding methods exist for rapid or inexpensive inbreeding, such as bulk breeding or single-seed descent. In single-seed descent breeding, a breeding population is successively self-pollinated several generations by saving only one seed from each plant at each generation and testing is not initiated until an advanced stage of inbreeding is achieved. The term, single-seed descent, was originally coined by Johnson and Bernard (1962), but the concept appears to have been introduced by Jones and Singleton (1934) and Goulden (1941). The advantages of single-seed descent include reduced time and labor in advancing generations, multiple generations per year, little record keeping, efficient selection for highly heritable traits that can be done on a single-plant basis, and efficient selection in later generations because it is best for crops with predominantly additive genetic variation (Brim, 1966). In later generations, additive genetic variation increases among lines and reduces within lines.

Related to the concept of single-seed descent and a recurring topic in selection during the past 50 yr has been the production and use of doubled haploids either as selection units themselves in self-pollinated species or as lines that can be used to produce selection units (Seitz, 2004). The major difference between doubled haploidy and single-seed descent is less opportunity for recombination of linked genes in the doubled haploids. Also, doubled haploids can be used effectively in crops with long generation times. The most recognized advantage of doubled haploids in plant breeding is the rapid attainment of complete homozygosity (e.g., rapid inbreeding) that makes doubled haploidy a particularly effective approach for crops with long generation time. Although the potential of haploid breeding was recognized as far back as the 1920s (Blakeslee and Belling, 1924) and haploid breeding was used in maize in the 1940s and 1950s to produce useful inbreds (Chase, 1951), before 1980 doubled haploid techniques were applied only to a small number of species. But during the past two decades the number of species amenable to doubled haploid techniques has increased to >250 (Maluszynski et al., 2003). At least one U.S. commercial seed company is now using the doubled haploid technique exclusively to generate new inbreds of maize (Seitz, 2004).

Returning to the question of what has changed during the past 50 yr with respect to selection units, the answer could be "not much." Certainly, our understanding of the relationship between line per se and testcross performance has improved, and the advantages of early testing have been more clearly demonstrated in cross-pollinated crops. But in hybrid crops, testcross progenies were the preferred type of selection unit 50 yr ago and the same is true today. Although early generation testing may be more prevalent today, especially with relatively recent adoption of short-cycle recurrent selection procedures in some self-pollinated crops, the concept predates 1956. Perhaps the most significant change has been in later generation testing in self-pollinated crops and the advancements in rapid inbreeding using single-seed descent and doubled haploid technology. However, the long-term impact of doubled haploids as selection units across many crop species has yet to be fully determined.

Selection Criteria

Although choosing the type of selection unit is an important component of selection, true selection for many plant breeders is represented by the selection criteria and methods they use to choose the best among the selection units. Much of the discussion about selection criteria in the past five decades has been on four topics—methods to improve selection efficiency and genetic gain, selection indices, indirect selection, and genotypic stability. Fundamental to understanding how to improve selection efficiency are the concepts of genetic gain and heritability. The phenotype (P) is determined by the genotype (G), the environment (E), and the interaction of the environment with the genotype (G × E). Simply, P = G + E + G × E + error. Broad sense heritability is the genotypic variance divided by the phenotypic variance. Narrow sense heritability is the additive genetic variance (the genotypic variance is due to additive, dominance, and epistatic genetic variance) divided by the phenotypic variance. Any tool or procedure that can reduce the environmental or unknown (error) variances relative to the genetic variance of the phenotypic variance will increase heritability and the gain from selection (Baenziger and Peterson, 1992).

Some of the methods that have been developed during the past 50 yr to improve heritability include the use of a grid in mass selection in maize (Gardner, 1961), advanced statistical designs, improved assays, and selection nurseries. Although advanced statistical designs were clearly developed years ago (Federer, 1955), the last 50 yr has greatly improved our methodology and our ability to use those methods (Stroup et al., 1994). In the area of improved assays, many of the biochemical and molecular genetic assays have improved selection efficiency by increasing the precision of measuring genetic value. For example, in wheat, many diseases have pathotypes with similar phenotypes, which complicates breeding for resistance. By knowing which disease pathotype is attacking the plant, it is easier to breed for resistance using the gene-for-gene concept. Similarly, understanding seed storage protein electrophoretic bands can help breeders understand the genotypes affecting the measured phenotype (Graybosch, 1992). Other technologies that are being developed to increase selection efficiency include those based on evaluating plant materials for specific traits and seed sorting based on near infrared reflectance (NIR) or transmission (NIT) technology. For

example, NIR can be used to identify kernels with differing kernel color (Wang et al., 1999a, 1999b) and starch properties (Delwiche and Graybosch, 2002), kernels that contain rye translocations (Delwiche et al., 1999), kernels that are diseased (Dowell et al., 2002, 1999), and kernels that have different protein contents (Bramble et al., 2002), end-use quality attributes (Delwiche et al., 1998), or kernel vitreousness (Dowell, 2000). One advantage of NIT technology is that it is nondestructive and multiple assays can be performed on an intact grain sample. Therefore, the breeder can directly use the selection units in further breeding operations. Also, sample preparation is quick and relatively inexpensive. Hence, these assays can be done on the scale that plant breeders need to evaluate many lines, especially when seed or plant materials are limited. With the ability to sort kernels on the basis of these traits, plant breeders will be able to enrich segregating populations for the traits that they desire.

Another way plant breeders have increased selection efficiency has been by modifying or deliberately choosing selection environments to allow better differentiation of selection units. A selection environment is one in which the environment is deliberately chosen to best differentiate lines (Brown et al., 1983; Baenziger and Peterson, 1992). A common example of this approach is the artificial infestation or inoculation of a nursery with a pest insect or a pathogen. During the past 50 yr, improved techniques for artificially rearing and infesting pests and inoculating pathogens have resulted in development of many cultivars of many crop species with enhanced levels of resistance. Another example of this approach has been winter wheat breeders choosing to locate a selection nursery in a location with a high probability of a harsh winter to ensure that all lines that survive would have an acceptable level of winter hardiness. Any lines that survive in the selection nursery will be able to survive in more normal production conditions and obviously lines that die during this selection are unavailable for advancement. A selection environment may not be representative of the evaluation environments. Evaluation environments are environments that are chosen to determine the areas of adaptation for a genotype, basically where the genotype can or cannot be successfully grown.

The concept of using a selection index to allow selection for multiple traits and/or multiple types of selection units predates 1956. Although the Smith-Hazel index remains the best index in theory (Bernardo, 2002), exact determination of the selection weights requires not only economic weights, but also error-free estimates of phenotypic and genetic covariances. Obtaining the latter estimates can be particularly difficult. This difficulty led to a series of simplified indices being introduced in the 1960s and 1970s. Among these were the base index in which economic weights are used directly as the weights (Williams, 1962), a multiplicative index using independent culling levels (Elston, 1963), a desired gains index that eliminated the need for phenotypic covariances (Pesek and Baker, 1969), a retrospective index that eliminated the need for genetic covariances (Allaire and Henderson, 1966), and a heritability-based index (Smith et al., 1981), in which the weights were a product of estimates of heritability and economic values. Although selection indices do have limitations (Baker, 1986; Wallace and Yan, 1998), empirical data have demonstrated that all of the various types of selection indices, if judiciously applied, can help the breeder meet selection objectives.

Indirect selection occurs when a trait other than the trait of primary interest is the selection criterion. Enhancing yield by modifying traits other than yield has been an approach long used by plant breeders. Probably the best-known example in recent history was the development of low-stature rice and wheat cultivars during the 1950s and 1960s (Jennings, 1964; Reitz and Salmon, 1968). The worldwide importance of these cultivars certainly led to an increased interest in ideotype breeding, which was described by Donald (1968) as an effort to increase yield by selecting for a series of plant characteristics, each of which has a specified goal and which collectively define the ideotype. Despite the increased interest in ideotype breeding in the 1970s and the awareness that in numerous species newer cultivars differed from older cultivars in certain plant characteristics [fewer tassel branches and more erect leaves above the ear are two examples in maize (Duvick et al., 2004)], successes from using this breeding approach exclusively have been few. Possible reasons for this outcome include size symmetry or compensation of plant parts, pleiotropy, and the genetic background (Rasmusson, 1987).

Perhaps no other topic of selection has been more discussed during the past decade than marker-assisted selection (MAS), which typically involves both indirect selection and a selection index. It is indirect selection because selection is usually for one or more markers that is closely linked to a gene (or a group of genes) that controls the inheritance of the trait of interest. Marker-assisted selection is most effective when the marker is closely linked to the gene controlling the trait and that gene has a large effect. When there are perfect markers (the marker could be the gene itself or a DNA sequence within such a gene; Ellis et al., 2002), plant breeders can directly select for the gene (e.g., selecting for reduced height genes; Peng et al., 1999). The use of such perfect markers is likely to become more common as more genes are isolated. Marker-assisted selection is a form of index selection when information on multiple markers and often the phenotypic values, as well, are used simultaneously to define a selection criterion. Although there are some reports of using markers to increase selection efficiency of polygenic traits (Stuber, 1994; Eathington et al., 1997; Young, 1999), the number of successes has been relatively few. The number of successes may increase as more high-resolution QTL maps, higher throughput marker technology, and integration of functional genomics with QTL mapping are developed (Collard et al., 2005), although the usefulness of MAS to improve polygenic traits in the long term has been questioned (Bernardo, 2001).

However, marker-based index selection to improve polygenic traits has not been the most common use of MAS. Much more common has been using markers to

accelerate the transfer of one or a few donor genes into a recipient genotype in backcross selection. Frisch et al. (2000) used simulation studies to show that the number of backcrosses needed to recover >95% of the donor genotype can be reduced from six with conventional backcrossing to three with use of markers. Reports of successful marker-assisted backcross selection include the transfer of desirable fruit traits in tomato (Bernacchi et al., 1998; Lecomte et al., 2004) and of the introgression into maize of a major gene affecting resistance to maize streak virus (Ribaut et al., 2002). Molecular markers will also prove invaluable in pyramiding genes with the same phenotype, such as disease or insect resistance genes. Another common way in which markers have been used to improve selection efficiency is indirect selection for qualitatively inherited traits in which the trait is difficult to score phenotypically. An example was selecting for the *b* allele of the *Ep-A1* isozyme to identify lines of wheat resistant to sharp eyespot [incited by *Pseudocercosporella herpotrichoides* (Fron) Deighton], as it is more efficient than screening using the pathogen (Koebner and Martin, 1990). Finally, molecular markers are routinely used by companies to fingerprint commercial cultivars to protect their intellectual properties.

Choosing environments in which to evaluate genotypes also can be viewed as an issue of indirect selection. The goal is to choose a set of evaluation environments in which genotypic performances are positively correlated to those in the target environments, which often can be only conceptually known. This approach requires some description of the G × E interaction. Most frequently during the past 50 yr, this interaction has been described via numerous statistical approaches, which include analysis of variance, linear regression on an environmental index, and various types of multivariate analyses (Crossa, 1990; Gauch and Zobel, 1996). The usefulness of these different approaches depends on the complexity of the G × E, with multivariate approaches being more appropriate for interactions of high dimensionality. In the past two decades, there has been an increased focus on using crossover interactions (a type of G × E in which significant changes in genotype ranks occur across environments) to classify environments (Baker, 1988; Crossa et al., 1993; Russell et al., 2003). Genotype × environment interactions also have been described by measuring actual attributes of the environment (Wood, 1976; Beckett, 1982; Baker, 1990). Such direct assessment of the underlying environmental variables that elicit G × E may be required for breeders to fully understand and use repeatable components of this interaction (Basford and Cooper, 1998).

Regardless of whether selection is direct or indirect or for a single trait or an index of traits, the overall criterion is for high mean performance. However, in addition to high mean performance, plant breeders also are concerned about the consistency of a genotype's performance across environments, which is referred to as genotypic stability. Considerable confusion has surrounded this issue, which undoubtedly is attributable to the myriad of stability parameters that have been defined. Lin et al. (1986) reviewed nine of these parameters and attempted to resolve some of the confusion by categorizing them into three concepts of stability. However, there still does not appear to be a consensus among plant breeders as to what constitutes a stable variety or to whether selection for stability should be a selection goal (Kang, 1993) or not (Baker, 1996).

Plant selection can be described quite simply as "keep the good and discard the rest" and simple visual selection by an experienced plant breeder remains as a rapid, inexpensive, and often highly effective approach. Nonetheless, during the past 50 yr, plant breeders have continually attempted to increase the efficiency of selection via application of new tools, such as the use of selection indices, and new technologies, such as seed sorting and MAS. Some of these already have had a significant impact. For others, the true impact will be determined as the next 50 yr unfold.

CONCLUSIONS AND LOOKING TO THE FUTURE

As we review the past 50 yr of Crop Breeding, Genetics, and Cytology (C-1), a number of trends emerge. First, our understanding of germplasm and how to manipulate it has greatly expanded. Once species were defined as populations that were able to be interbred, but were reproductively isolated from other populations (Rieger et al., 1976). However, many species can now be hybridized to improve plants using embryo rescue, occasionally colchicine to double chromosomes, and chromosome pairing genes that allow mispairing and recombination. Even where species barriers remain, genetic transformation has made the complete biosphere our source of genes and even this is too small for our real gene pool as synthetic genes are created.

In 1955, qualitative (Mendelian) and quantitative genetics were viewed as largely two distinct fields that must be related, but the bridge between the two was truly an enigma wrapped in assumptions. The last 50 yr has lead to an unprecedented understanding of what genes are and how they interact with each other and the environments to explain continuous variation through chromosome loss, substitution, and addition lines; QTL analyses; microarrays; and improved statistical models. The genes that are the basis of the Green Revolution, previously described by their response to simple plant hormones, have been cloned and their gene action elucidated (Peng et al., 1999; Ueguchi-Tanaka et al., 2005). Simply, we are poised at the DNA level to understand the genes affecting the traits that feed the world. However, this understanding by itself will not be sufficient to effect real-world improvements. Plant breeders and plant production specialists have worked to create systems where genes can be effective. For example, the semidwarfing genes in wheat were present in many older Italian cultivars (Reitz and Salmon, 1968), but had little selective advantage until the production system highlighted their strong straw. Furthermore, having the gene and creating new cultivars with the gene (e.g., having

the gene in the right background) require related, but different efforts, though transformation may draw these research efforts closer. The plant breeder remains the one who has to decide the breeding objectives, select the parental germplasm, and manipulates thousands of genes to create the genotype that gives that desirable phenotype. The plant breeder will continue to handle large populations, so visual selection remains critically important as a rapid, inexpensive selection tool. Selection efficiency has been and will continue to be improved through better diagnostic tools which remove phenotypic uncertainty, increase heritability of the trait, and provide better selection gains. Marker-assisted selection has aided both in tracking the gene and rebuilding the background in backcrossing programs. Greater mechanization, computerization, and optical sorting that enrich populations for selected traits have not only improved selection efficiency, but removed some of the skill and drudgery of plant breeding. Modern combines can cut plots and save or discard them on the basis of how the plots relate to known check cultivars in the field. Data is virtually instantaneously sent to data hubs for analysis and returned to plant breeders. This technology is a far cry from when we marveled at computers and keypunch cards or the first hand held calculator that could do an analysis of variance. Similarly, breeding theory and practice have been enhanced greatly by breeding simulations and new data analyses (mixed models, stability analyses, etc.) that were not previously amenable without better computers. Finally, plant breeding is by nature a forward-looking science that must predict what the future needs will be. As better crop models are developed and more genomic information become available, we may be able to both predict the future plant types and genotypes that are needed (Baenziger et al., 2004).

An appropriate conclusion to this review of the last 50 yr of crop breeding, genetics, and cytology is to comments on who will be doing plant breeding in the future. As plant breeders become more efficient and their industry consolidates, there may well be fewer of us. There may be more geneticists as our genetic understanding increases. Clearly there is a need for more research teams that cover the broad spectrum of breeding, genetics, and cytology, as well as other fields. It should be recognized that many developed countries view agriculture as a constant source of government intervention and subsidy. In less developed countries with critical needs to feed people, agriculture involves more of the population and is considered vital to national security. It may be that much of the clever, resource-limited research in plant breeding, genetics, and cytology will reside in those less developed countries where resources are limited, but patience abounds. It is not by chance that hybrid cotton, rice, and wheat are most widely grown in emerging economies rather than developed economies.

Finally the greatest constant in plant breeding, genetics, and cytology is the simple joy of creating new knowledge and occasionally new cultivars that make a difference and improve lives.

EPILOGUE

"We shall not cease from exploration,
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time."
—From *Little Gidding* by T.S. Eliot

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